

Factors Influencing Plant Productivity in Shrub Communities on Elk Winter Range of Rocky Mountain National Park: Experiments on Elk Herbivory, Water Availability, and Burning

By

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Abstract. Elimination of large predators and reduced hunter harvest has led to concerns that an increasing elk (*Cervus elaphus*) population may be adversely affecting vegetation on the low elevation elk winter range of Rocky Mountain National Park, Colorado. Vegetation production and nutrient responses to herbivory, water availability, and burning were studied over a 5-year period to determine the effects of these processes on willow (*Salix* spp.) and bitterbrush (*Purshia tridentata*) communities.

Elk herbivory suppressed willow heights, leader lengths, and annual production, as well as herbaceous productivity of willow sites. Water impoundment had a positive effect on herbaceous production ($P < 0.05$), but little effect on shrubs in willow sites. Water impoundments on drier sites increased graminoid production over sites that had naturally high water tables. Surveys conducted to evaluate current beaver numbers and distribution documented a 94% population decline on the elk winter range since 1940, indicating the potential for altered hydrologic regimes in the past 50 years.

Burning in upland bitterbrush communities decreased amounts of shrub cover and production, but had no apparent effects on herbaceous standing crop biomass, with the exception of *Stipa comata*, which had lower production after burning ($P < 0.001$) and the carbon content of summer grasses. Grazing resulted in decreased herbaceous standing crop biomass, increased nitrogen content of upland grasses, and increased dry matter digestibility of forbs and grasses.

Vegetation conditions in willow sites on the elk winter range appear to be affected by a number of factors, of which elk herbivory is only one. Elk herbivory appears to be the predominant force in determining vegetation productivity in willow sites, but its effects may be exacerbated by lowered water tables. Restoration of fire through prescribed burning to bitterbrush communities does not appear to be effective in increasing herbaceous forage production; however, the majority of burns took place in spring when there was little fuel to carry a fire. Fall burns may prove more effective.

Keywords: Beaver, *Cervus elaphus*, herbivory, hydrology, national park management, prescribed fire, *Salix*.

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Introduction

Native large mammalian herbivores significantly influence plant species abundances and ecosystem processes (McNaughton 1984; Hobbs 1996). However, human developments can concentrate animals onto smaller ranges, thus increasing population densities while diminishing forage availability, and may decrease movements between, and within, seasonal ranges, potentially changing the scope of herbivore influence. Additionally, human manipulations of landscapes, such as the draining of wetlands for agricultural purposes and planting of crop species, can alter the plant communities on which herbivores rely. These influences may combine to create situations where less common plant communities and associated animal species are altered due to increased herbivory, competition from non-native or grazing-resistant plant species, and changing environmental and climate conditions.

Ideally, national parks and other protected areas should be pristine areas where habitats are protected from "unnatural" influences. However, many of these areas have been subjected to extensive human alterations, either presently or in the past. Therefore, many of the ecosystems represented in these areas are missing important elements, including key predators and other animal species; an intact complement of native habitats, including healthy riparian areas; and plant communities unaltered by exotic species (Huff and Varley 1999; Wright 1999).

The impact of ungulate herbivory on plant production has been hotly debated. Several researchers have demonstrated "grazing optimization", where plant productivity increases in response to grazing through overcompensation of the plant for tissues lost to herbivores (McNaughton 1979, 1984; Dyer et al. 1991). However, application of this theory to U.S. western rangelands was questioned by Painter and Belsky (1993), Patten (1993), and Bartolome (1993). DeAngelis and Huston (1993) pointed out the importance of physiological characteristics and environmental conditions in response of individual plants to herbivory.

Broad-scale declines in willows (*Salix* spp.) have occurred at a number of locations in the Intermountain U.S. West where there are also dense ungulate populations (Boyce 1989; Singer et al. 1994). Elk (*Cervus elaphus*) are protected at some of these locations, such as in national parks and the National Elk Refuge, Wyoming. Predators were eliminated at some of these sites and considerable confusion exists over what effect predators and Native Americans might

have had in regulating or limiting the abundance of elk (Kay 1990, 1994; Wagner et al. 1995a; McNaughton 1996; Singer et al. 1998a). Willow declines in the presence of high elk densities have been documented in Rocky Mountain National Park (RMNP) and Yellowstone National Park (YNP) (Singer et al. 1998b; Zeigenfuss et al. 1999) and the National Elk Refuge (Smith and Robbins 1994). All of these areas have similar histories of human alterations of the landscape and hydrologic conditions. The climate has become warmer and drier throughout the century, thus contributing to willow declines in YNP and RMNP (Balling et al. 1992; Singer et al. 1998b). Beaver declines have also been documented in both of the parks on their major elk winter ranges (Consolo-Murphy and Hanson 1993; D. Stevens and S. Christianson, Rocky Mountain National Park, unpublished report).

Willows typically become established on disturbed sites with abundant water. Willows are adapted to outgrow the reach of ungulates and to out-compete neighboring plants through rapid vertical growth rates and large belowground storage of nutrients and energy (Bryant et al. 1983). A more arid climate might reduce water availability to willows. Cooper et al. (1998) found that in a dry year in RMNP, water tables in a restored area previously drained by ditching dropped to a degree similar (40–70 cm) to pre-restoration levels. It could be assumed that this dry climate effect would be exacerbated in areas where natural flows had not been restored over longer periods of arid conditions. Beaver declines may also contribute to willow declines. Beaver populations play important roles in channel geomorphology, increasing water tables, retention of sediment and organic matter, modifying nutrient cycling and decomposition, and habitat modification, including community and species compositions (Naiman et al. 1986). Climate change, increasing elk numbers, and beaver declines varied this century (Singer and Cates 1995; Wagner et al. 1995b) and potentially interacted in their impacts on ecosystem processes. Thus, any research other than experiments planned to differentiate these effects are unlikely to shed further light on the factor(s) most responsible for willow declines.

Water stress may act to make plants more vulnerable to herbivory and reduce the ability of a plant to compensate for tissue losses. Physiologically stressed plants may produce less total resin and phenols compared to healthy plants (Kozlowski 1971; Singer et al. 1994, 1998b; Cates et al. 1999), and thus may be fed on preferentially by herbivores (Gurchinoff and Robinson 1972; White 1984; Halls et al. 1994; Swihart and Picone

1998). Herbivory may interact with water stress in a number of ways. Herbivory may lower shoot/root ratios, thus reducing the transpiration tissues (leaves, shoots) and improving the water status (i.e., reducing water stress) of the grazed plants (Wright et al. 1989). Where most of the plants are grazed, such as in the Serengeti grasslands, the reduction in overall transpiring plant tissues may serve to increase soil water and extend the growing season (Georgiadis et al. 1989). However, herbivory and water stress may also interact to reduce the long-term ability of the plant to recover. Browsed willows in RMNP apparently have less access to the ground water table than unbrowsed willows, suggesting that browsed willows have lost root structures that had access to the water table (Menezes et al., this volume).

Fire also plays an important role in plant production by releasing nutrients to the soil in a more accessible form for plant uptake, as well as introducing structural heterogeneity to the plant communities. Wildfires have been suppressed in RMNP for most of its history, and until recently, prescribed fire has not typically been used as a management tool.

Management of elk and vegetation in Rocky Mountain National Park, Colorado has been an issue since the 1930s. Elk populations were maintained at constant levels through removals by park management from the 1930s–1967, but have increased about 3-fold since the cessation of artificial controls within the park boundaries in 1968. Park managers are concerned that possible unnatural concentrations of elk may alter natural plant communities and ecosystem sustainability. Concerns over possible further elk increases and concurrent vegetation declines [particularly in willow (*Salix* spp.) and aspen (*Populus tremuloides*) communities on the winter range] have been expressed in recent years (Olmsted 1979, 1980; Hess 1993). Analysis of vegetation conditions on the winter range from 1968–1992 led former park biologist, David Stevens, to conclude that only willow and aspen stands on optimum habitat would survive under current browse pressure (D. Stevens, National Park Service, unpublished report).

Changing vegetation conditions may be a natural product of climate change, human-induced changes, hydrologic changes, fire suppression, or an expected result of recovery of elk to greater densities following cessation of artificial controls. All of the meadows that make up the significant proportion of elk feeding areas on the park winter range were altered throughout this century by extensive hydrologic changes. Direct human-induced alterations included: drainage and irrigation for cultivation; water removals to support homesteads,

lodges, and National Park Service (NPS) administrative and visitor facilities; and water rights diversions. Beaver declines resulted in altered stream courses, dry channels, and drained ponds. Elk were absent, or their populations controlled at low densities, for over half a century (late 1800s to 1969). Vegetation conditions and succession may have changed because of underpopulation of a large native herbivore. Some vegetation changes observed since 1969 might be interpreted as a return to more natural conditions (pre-European settlement) with the return of elk to a more significant role in the ecosystem. Vegetation conditions may not be declining beyond natural conditions to be expected from elk grazing (Houston 1982).

Upland bitterbrush communities make up 50% of the feeding areas within the park's elk winter range. Elk utilize the understory grasses to a great extent in the winter, removing approximately 60% of growth annually (Singer et al., this volume). Previous studies have shown that since elk were released from artificial controls, percent of cover of bare ground on grasslands has increased (Zeigenfuss et al. 1999), and in bitterbrush areas, shrub cover is increasing. Stevens (unpublished report) observed that grasslands predominate with the disturbance of fire or heavy ungulate grazing. Grasslands may be decreasing and shrub cover increasing on xeric sites due to fire suppression policies that have prevailed in the park since its establishment. There has also been concern over the potential for shifts in species composition towards more palatable, grazing-resistant species, such as *Poa pratensis*, *Phleum pratense*, and *Koeleria macrantha* because of high levels of grazing.

We addressed the major issues of herbivory, water availability, and fire through a series of controlled experiments based on the following hypotheses:

- (a) Plant productivity has declined due to elk. It will increase when elk are excluded and levels of herbivory that are higher than ambient levels will decrease plant productivity.
- (b) Production in willow sites will respond positively to increased water availability. Willow sites with high water tables will better sustain elk herbivory as reflected by increased willow production, willow heights, and herbaceous production.
- (c) Plant species composition has been altered by several years of elk herbivory. Excluding elk herbivory will result in shifts in plant species diversity.
- (d) Beaver populations have continued to decline over the past 17 years.

- (e) Plant production and shrub cover in bitterbrush sites will respond positively to prescribed burning. Initial increases in herbaceous plant production and eventual increases in cover of bitterbrush will follow burning. Quality of forage in burned sites will increase as reflected by increased nitrogen concentration and dry matter digestibility of forage.

Study Area and Treatments

Sixteen study sites were randomly selected in the elk winter range of the northeastern side of RMNP in the montane riparian and upland shrub communities. Vegetation communities were identified and random points generated in each vegetation type using a Geographic Information System (GIS).

Twelve study sites were located in riparian willow communities of: (1) the north and south sides of the Moraine Park area of the Big Thompson River drainage of the Big Thompson watershed (elevation 2,481 m); and (2) the Horseshoe Park area of Fall River drainage of the Big Thompson watershed (elevation 2,598 m). Predominant willow species throughout all areas were *Salix monticola*, *S. planifolia*, and *S. geyeriana* mixed with other mesic shrubs, such as *Potentilla fruticosa*, *Betula glandulosa*, *B. occidentalis*, and *Alnus tenuifolia*. Eight of these sites (four in Moraine Park and four in Horseshoe Park) were located in drier areas with little or no current beaver activity that supported short, heavily browsed willow. In all of these "short willow" sites, evidence from dead and decadent willows indicates that plants over 2 m tall were once present on all of these sites. The other four sites (two in Moraine Park and two in Horseshoe Park) were located in beaver-occupied areas (including areas of recent activity), or high water table areas, that supported taller willow plants subject to less severe hedging by the elk. These sites are referred to as "tall" willows.

Two 30.5 m x 45.7 m paired plots were chosen at each site. One randomly selected plot was fenced to exclude elk and deer and the other remained unfenced. Exclosures were erected in August–November 1994. In half of the sites with shorter willows (two in each drainage, $n = 4$), we attempted to raise the water table. This treatment, referred to as "short-watered" willows, was imposed in spring 1995. The treatments consisted of sheet metal check dams placed in both the grazed and ungrazed (exclosed) areas at each site. The dams were

placed in existing ephemeral stream channels to impede the flow of rain and snowmelt runoff and raise the water levels locally. The rest of the shorter willow sites (two in each drainage, $n = 4$) were left to their normal hydrologic regimes and referred to as "short-control" willows. Throughout the growing season, water table levels at all the sites were monitored using wells and by measuring water levels on either side of check dams. Annual herbaceous consumption averaged 55% of annual production and shrub consumption averaged 33% of current annual growth throughout the study period (Singer et al., this volume). Elk were the primary ungulate herbivore in these systems.

Within each willow exclosure, simulated browsing treatments were conducted during winter (January–March) each year. At the outset, each exclosure was divided into sections that were randomly assigned to a "clipped" treatment or an "ungrazed" treatment. The clipped treatment, from fall 1995 onward, consisted of clipping 75% of the current year's growth from all forage shrubs and clipping 75% of the herbaceous layer in that section of the exclosure. This was intended to simulate greater herbivory that might occur with an increase in elk numbers or concentrations and to test the effects of these higher consumption levels. All clipped plant material was removed from the exclosure. Ungrazed treatments were unmanipulated areas within the exclosures. The grazed (unfenced) plots were left to unregulated elk grazing and browsing.

Four study sites were randomly located in upland communities. These sites were all located on southern exposures in the areas of Hallowell Park (elevation 2,652 m), Deer Ridge (elevation 2,591 m), Aspenglen Campground (elevation 2,500 m), and the Beaver Meadows Entrance Station (elevation 2,454 m). Primary vegetation cover consisted of antelope bitterbrush (*Purshia tridentata*) and mountain muhly (*Muhlenbergia montana*) associated with sparse ponderosa pine (*Pinus ponderosa*). These sites were established to study the effects of herbivory and prescribed burning on production and species composition in this vegetation type. Two 30.5 x 45.7 m paired plots were chosen at each site. One was randomly selected to be fenced to exclude elk and deer and the other was open to grazing and browsing. Exclosures were erected in March–May 1995. Half of the area inside and outside exclosures at each site was burned in late fall 1995 or late April/early May 1996. Annual herbaceous consumption averaged 60% and shrub consumption averaged 12% throughout the study period (Singer et al., this volume).

Methods

Hydrological Monitoring

Area snowpack (at the Willow Park SNOTEL site) data were obtained from the USDA Snow Survey Office and growing season precipitation data from Colorado Climate Center's Estes Park site. The Willow Park SNOTEL site is located 9.2 km east of Horseshoe Park, at the head of the Fall River drainage. During the 1997 growing season, rain gauges were maintained within Moraine Park and Horseshoe Park. Simple open-top gauges were placed in open, unobstructed areas and read at least once every 2 weeks, depending upon rainfall events. River levels were monitored during the 1997 growing season. Metal bars were placed in river channels at the study sites in both watersheds. The top ends of these bars were surveyed with reference to an arbitrary elevation plane. Measurements of river levels were made every 2 weeks.

In the summer of 1994, 81 shallow wells were installed in the two watersheds under investigation to monitor seasonal and annual changes in water levels, as well as those induced by our damming treatments. Fifty wells were placed in the Horseshoe Park willow study sites and 31 in the Moraine Park willow study sites. Wells at most sites were placed along site boundaries both parallel and perpendicular to the flow of water through the site. Wellheads were referenced to the same arbitrary plane of elevation as the river channel bars. Depth of penetration for the wells varied from less than 1 m to just over 2 m below the surface. Depth of wells was determined by the maximum depth that could be reached using a gas-powered auger, or 0.5 m past the first sign of the water table. Wells were constructed of 2-inch diameter PVC pipe slotted along the entire length that was underground. During the growing seasons from 1995 to 1998, groundwater levels were read at least once per month at all sites, usually coinciding with the reading of river levels. It was not possible to collect pre-treatment groundwater data prior to the installation of the check dams, so we compared them to undammed short willow sites nearby.

Beaver Surveys

Beaver surveys were conducted on 11 streams within the Big Thompson River watershed in the northeastern portion of the park. Field surveys were conducted from October 1994 through December 1998 repeating similar

ground surveys conducted in 1939–1940 (Packard 1947), 1964, and 1980–1981 (Rocky Mountain National Park, unpublished data). We surveyed stream reaches in which beaver activity had been reported in the prior surveys, mapping the location of signs of current beaver activity, including fresh cuts on vegetation, food caches, and lodges and dams with fresh work or vegetation cuttings from the current year. Surveys were conducted during all months, but were concentrated between October and May when frozen stream channels facilitated walking.

We compared the number of lodges recorded for the most recent survey of each stream with the number recorded for the same areas in the earlier surveys. We estimated the population size for each stream based on an assumed colony of six beavers per lodge following prior surveys. Where current activity was evident but no lodge located, we assumed one active colony of six beavers. We compared the estimate based on our most recent survey to 1939–1940, 1964, and 1980–1981 estimates.

Shrub and Herbaceous Production

Three 9.3 m² randomly-selected circular plots were established in each treatment at each study site in 1994 for measuring shrub production. Data on shrub production were collected in the late summers of 1994–1996 and 1998 for willow sites and 1994–1997 for bitterbrush sites. Data collected on each plant included species; canopy diameters (widest and perpendicular to widest diameter); plant height; number of stems; and an estimate of percent of canopy dead. On every fourth individual of each shrub of each species, a subsample of the number of browsed and unbrowsed leaders; diameters at twig base, tip, and point of browse (grazed plots only); and leader lengths (1996–1998) were also collected. Several willows ($n = 2-4$) of the three predominant species in each treatment at each enclosure were also tagged for more intensive measurement throughout the course of the study. Catkin production was measured in June 1996 and 1998 on tagged plants. Annual aboveground production was estimated using log-log predictor regressions of total production (dependent variable) on canopy volume (independent variable) of willows and bitterbrush following Peek (1970). Plant material removed from the tagged plants during annual willow clipping treatments was collected for use in creating regression models. A number of willow and bitterbrush plants located outside the study sites, but within close proximity to them, were sampled for plant production in late summer 1995 and 1996. These samples included leaves and twigs and were

used to determine corrections for total plant production since samples taken during establishment of clipping treatments were winter samples that contained twigs but not leaves.

Regression equations were developed to predict willow production for the three major willow species (*Salix monticola*, *S. planifolia*, *S. geeyeriana*) found in our study sites. Equations were developed separately for 1995 and 1996 for Moraine Park and Horseshoe Park. Data from these 2 years was pooled to create equations used to predict total willow production for 1994 and 1998 since tagged plant production samples were not available for these years. R^2 values for these equations were high and ranged from 0.75 to 0.92 (Table 1). To determine if these equations were suitable to cover a range of willow morphology, we tested for differences in slopes of the regression lines between models for tall (>125 cm) and short (<125 cm) willows, ungrazed and grazed willows (1995 data only), and Horseshoe Park and Moraine Park samples. While few differences were observed in any of these cases, we did develop separate regressions for Moraine Park and Horseshoe Park because of differences in elk density, elevation, and hydrology between these areas and based on the literature where separate regressions are often developed for separate study areas (Peek 1970).

Pre-treatment herbaceous standing crop biomass data were collected by clipping five randomly located 0.25-m² circular quadrats in late summer 1994 in each treatment at each study site. In July–August 1995–1996 and 1998 for willow sites and 1995–1997 for bitterbrush sites, three 0.25-m² circular quadrats were randomly placed in each treatment at each site to measure annual herbaceous standing crop biomass. In the grazed treatment, biomass was sampled from beneath 1-m² movable grazing exclosures that had been randomly placed at the beginning of the growing season. All graminoids and forbs within the quadrat were clipped and sorted by species to measure annual peak production. Litter was also collected from within each quadrat. Vegetation was oven dried at 55°C for 48 hours and weighed. Visual estimates of percentage (to nearest 5%) bare ground, moss, lichen, cacti, and shrub cover were recorded for each plot, and a more intensive estimate of percent cover of species (upland bitterbrush) and major functional groups and substrate/ground cover (willow sites) was conducted in 1998.

Nutrient Analyses

Samples for nutrient analyses were obtained from the tagged willows in August 1998 and January 1999. Composite graminoid and forb samples from the previous growing season were collected from grazed treatments in April 1998 (all sites). Composite samples from current graminoid and forb growth were collected in July 1997 (bitterbrush sites) and 1998 (willow) from all treatments. Samples were analyzed for carbon (C) and nitrogen (N) content using a LECO CHN-1000 Carbon Hydrogen and Nitrogen Analyzer. Dried and ground plant samples were combusted in a chamber and resultant gases passed through infrared cells to determine carbon, and through a thermal conductivity cell to determine nitrogen.

Percent dry matter digestibility of herbaceous plants and willows was analyzed using an in vitro technique that simulates natural ruminant digestion under laboratory conditions. Samples of known weight were inoculated with a rumen-buffer solution and digested for 48 hours at 39.5°C, centrifuged, an acid-pepsin mixture added to the sample after supernatant was discarded, and digested an additional 48 hours. Samples were then filtered and the percent digestibility determined by weight difference.

All samples from live grasses and forbs were analyzed for total non-structural carbohydrates (carbohydrates that are readily available as a source of energy to the plant—including sugars, dextrin, starch, and fructosan). Complete hydrolysis of the extracted carbohydrates to reducing sugars was accomplished using a mild 0.2 M sulfuric acid solution. The reducing power of the neutralized hydrolysates was then determined by titration with standardized sodium thiosulfate.

January willow twig samples were analyzed to determine content of a suite of macronutrients, including: calcium, phosphorus, potassium, iron, magnesium, manganese, sodium, zinc, copper, titanium, aluminum, nickel, lead, molybdenum, cadmium, chromium, strontium, boron, barium, silicon, and vanadium. Dried and ground 1.0 g plant samples were digested with 6.0 ml nitric acid and 2 ml of perchloric acid at 200°C until the volume was reduced to 2 ml. The samples were then cooled and diluted to 50 ml with deionized distilled water. The minerals were analyzed using an ICP-AES (inductively coupled plasma-atomic emission

Table 1. Regression equations developed for determining annual production from canopy volume for predominant willow species on low elevation elk winter range of Rocky Mountain National Park, Colorado.

Location	Species					
	<i>Salix geeyeriana</i>		<i>Salix monticola</i>		<i>Salix planifolia</i>	
	Regression equation	r ²	Regression equation	r ²	Regression equation	r ²
1996						
Horseshoe Park	$wt = e^{(3.896 + 0.766 \ln(vol))}$.82	$wt = e^{(3.435 + 1.175 \ln(vol))}$.75	$wt = e^{(3.539 + 1.063 \ln(vol))}$.79
Moraine Park	$wt = e^{(3.997 + 0.766 \ln(vol))}$.87	$wt = e^{(3.970 + 0.882 \ln(vol))}$.88	$wt = e^{(3.912 + 0.976 \ln(vol))}$.92
1995						
Horseshoe Park	$wt = e^{(3.568 + 0.756 \ln(vol))}$.75	$wt = e^{(4.070 + 0.591 \ln(vol))}$.75	$wt = e^{(3.768 + 0.908 \ln(vol))}$.85
Moraine Park	$wt = e^{(3.492 + 0.712 \ln(vol))}$.83	$wt = e^{(3.913 + 0.762 \ln(vol))}$.88	$wt = e^{(3.725 + 0.856 \ln(vol))}$.81
1994, 1998						
All	$wt = e^{(3.725 + 0.787 \ln(vol))}$.82	$wt = e^{(3.922 + 0.806 \ln(vol))}$.82	$wt = e^{(3.750 + 0.952 \ln(vol))}$.83

wt = production in grams

vol = canopy volume of shrub (m³)

spectroscopy). All dry matter digestibility, non-structural carbohydrate, and mineral analyses were performed at the Range Nutrition Laboratory at Colorado State University, Fort Collins.

Statistical Analyses

Statistical analyses were performed using SAS (version 6.12) statistical software. Shrub annual production, height, species-specific production, canopy area and volume, catkin production, and leader lengths were tested for differences between all treatments. Herbaceous standing crop biomass and species composition were also examined for treatment differences. Data from willow sites were analyzed for differences between all treatments using PROC MIXED in SAS, an analysis procedure that is a generalization of the standard linear model designed to analyze data generated from several sources of variation. This method allowed us to account for, and test for, the effects caused by the different watersheds (Moraine vs. Horseshoe), as well as random sites. Differences between individual means were determined using the probability associated with the *t*-statistic for pairwise comparisons between least square means. PROC GLM, the general linear model for data with only one source of variation, was used for analysis of data from bitterbrush sites since these sites were not grouped in watersheds, but randomly placed over the entire landscape of available bitterbrush. The F-protected least significant difference was used to determine significant differences between means. When the assumptions of equal variance were not met, variables were log transformed to stabilize variance. Comparisons between years were performed using only the ungrazed and grazed treatments. Due to the wide variability in sample means, differences between treatments were considered significant at the 90% confidence level ($P < 0.10$).

Because the water additions were limited in magnitude (12–37 cm) and duration (May and June only), we also investigated the response of willows to water through correlations of growth parameters to depth to the water table.

Results

Hydrological Monitoring

Above-average snowpack conditions existed at the beginning of the growing season for the first 3 years of the study (1995–1997). The water year 1998 snowpack

was similar to the 30-year average in magnitude, time, and duration. Figure 1 compares the 4 years covered by this study with the 30-year average for 1961–1990 for the area.

May through mid-June of the 1995 growing season was a period of above-average precipitation. Total precipitation for these 2 months was 20 cm above the 30-year average. This precipitation, combined with the heavy runoff from the above-average late season snowpack (Fig. 1), led to very high water tables in our study sites. The resultant high river levels made data collection difficult at some sites and led to the late-June flooding of at least one site in Horseshoe Park. The growing season precipitation total (May–September) for 1995 was 14 cm greater than the 30-year average. Totals for the next three growing seasons (1996–1998) were within 3 cm of the 30-year average. Rain gauge measurements in the 1997 growing season indicated very similar rainfall patterns and totals for the two watersheds (27.4 cm for Horseshoe Park and 26.5 cm for Moraine Park).

Dates of peak river levels varied, from early June in 1998 to the end of June in 1995, as a function of snowpack characteristics of that year (L. Zeigenfuss, U.S. Geological Survey, personal observation). The amplitude of river level change in Horseshoe Park was approximately twice that of Moraine Park, perhaps due in part to differences in channel morphology. Fluctuations in groundwater peaks and lows from year to year were the result of variations in timing and volume of snowpack runoff (May–June), and variations in precipitation inputs throughout the season (Fig. 2). Even

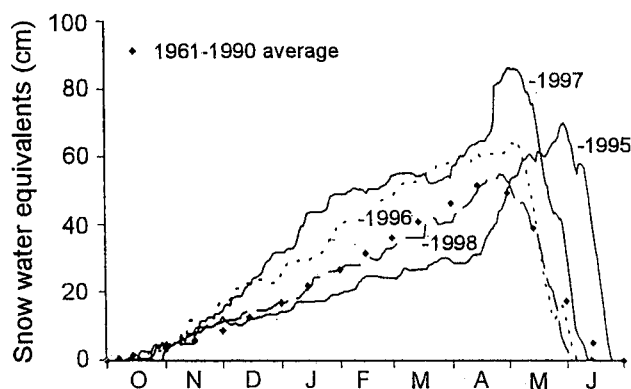


Fig. 1. Snowpack data for Willow Park, Rocky Mountain National Park, Colorado. Thirty-year average (1961–1990) compared to 1995–1998 Water Years. Source: USDA Snow Survey Office, Lakewood, Colorado.

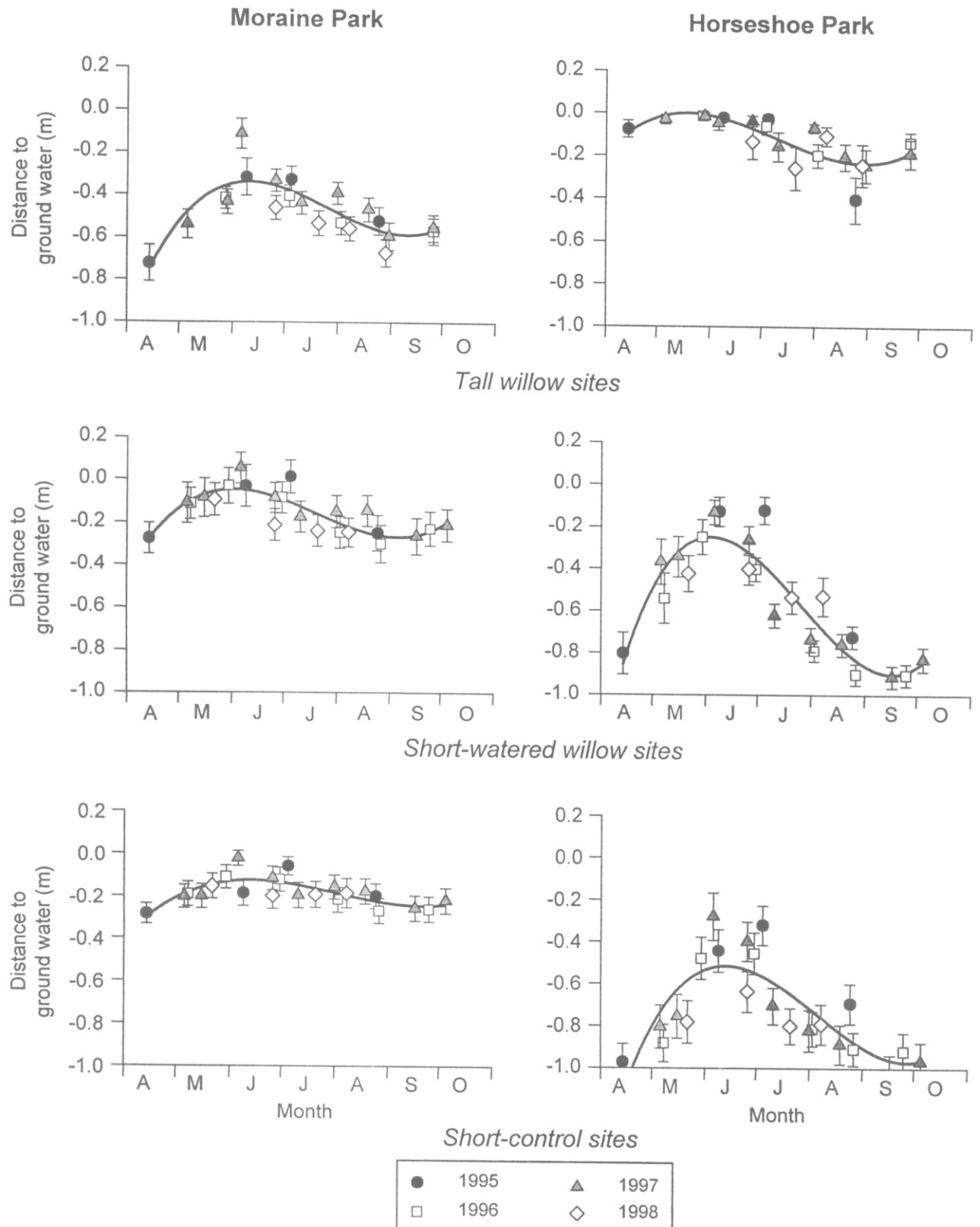
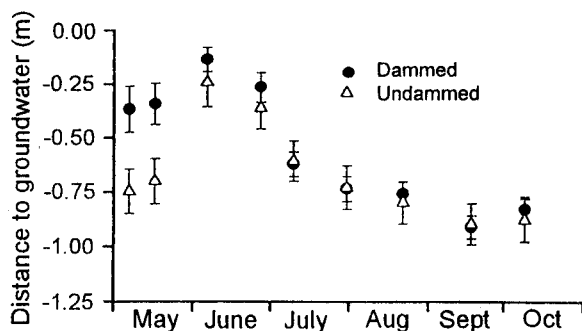


Fig. 2. Distance to groundwater in: (a) tall willow sites; (b) short-watered willow sites; and (c) short-control willow sites in Moraine and Horseshoe Parks, Rocky Mountain National Park, Colorado, 1995–1998.

when low rainfall conditions were experienced during July–September, groundwater levels never averaged more than 1 m below the surface. We hypothesized that tall willow sites would be wetter (i.e., that wetter conditions contributed to the presence of taller willows). Sites in Horseshoe Park followed the pattern we expected. Tall willow sites were the wettest, followed by short-watered sites, and short-control sites. However, this pattern was not present in Moraine Park where the short-control sites were wettest and the tall sites were the driest (Fig. 2). The check dams were successful in holding additional water at the sites during the early growing season. The mean difference between groundwater levels between dammed and undammed sites in May of 1997 was 37 cm for Horseshoe Park and 12 cm for Moraine Park (Fig. 3). Early season difference between water elevation in the channel behind the dam and that at the nearby intersection with the river was approximately 0.6 m. By early July, after spring run-off had subsided, water no longer backed up behind the check dams, and the difference in mean groundwater levels between short-watered and short-control willow sites had disappeared.

a. Horsetooth Park 1997



b. Moraine Park 1997

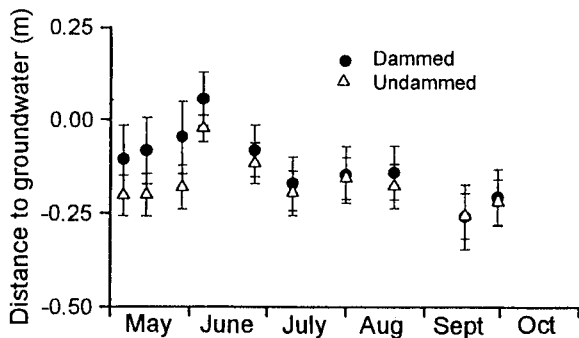


Fig. 3. Comparison of 1997 well measurements (mean \pm S.E.) for undammed and dammed willow sites in: (a) Horseshoe Park, and (b) Moraine Park, Rocky Mountain National Park, Colorado.

Within each park, significant differences ($P = 0.058$ for Horseshoe Park and $P = 0.038$ for Moraine Park) between groundwater levels in short-watered and short-control willow sites occurred at the beginning of the growing season (May), before the rise in river levels (Fig. 3). At the time of high river levels and the resultant higher ground water levels throughout the system (early June) the difference between damming treatments lessened but still existed.

While each site in the study was unique in its surface water and groundwater characteristics, all sites exhibited high groundwater levels in the first half of the growing season. At all sites, even the lower late-season groundwater levels appeared to be high enough to be readily accessible for willows and other deep rooted plants in the sites all years (Alstad et al. 1999). At some sites in years of low precipitation (1994, 1998), *Carex* plants further away from watered channels (which have shallower roots than willows) may have experienced periods of water stress during the later half of the growing season (Alstad et al. 1999).

Beaver Populations

Beaver activity occurred on 8 of the 11 streams surveyed. Since 1981, one stream (Hidden Valley Creek) was abandoned and colonies established on one unoccupied stream (Mill Creek). Two streams that were abandoned between 1940 and 1981 (Wind River and Beaver Brook) remained unoccupied.

The total number of active lodges declined 83% between 1940 and 1981, and an additional 12% by 1994–1998, resulting in an overall decline of 95% since 1941 (Table 2). Similarly, the total estimated population size on surveyed drainages declined 79% between 1940 and 1981, and an additional 15% by 1994–1998, resulting in an overall decline of 94% since 1941 (Table 2). Estimated population sizes declined on all streams except the North Fork of the Big Thompson. The largest declines occurred on the Fall River, Big Thompson River, Glacier Creek, and Mill Creek.

Plant Production and Nutrient Responses to Water Manipulations and Herbivory Treatments in Willow Sites

Grazing resulted in significantly lower willow production ($P = 0.017$) than ungrazed and clipped treatments by 1998 (Fig. 4). This difference only became

Table 2. Active beaver lodges and estimated beaver population size in the Big Thompson River watershed on elk winter range in Rocky Mountain National Park, Colorado.

Location	Active lodges			Estimated population size		
	1939–1940	1980–1981	1994–1998 ^a	1939–1940	1980–1981	1994–1998 ^a
North Fork	1	1	0	6	6	6
Cow Creek	4	2	2	24	18	12
Fall River (Horseshoe Park)	13	10	0	96	24	6
Hidden Valley Creek	10	2	0	70	6	0
Beaver Brook	6	0	0	36	0	0
Big Thompson River (Moraine Park)	52	3	2	315	18	12
Cub Creek	7	1	1	60	6	6
Mill Creek	22	0	2	144	0	12
Glacier Creek/Boulder Brook	18	4	1	150	24	6
Wind River	3	0	0	18	0	0
Total	136	23	7	919	195	60

^aNumbers reported are for most recent year surveyed in the period 1994–1998.

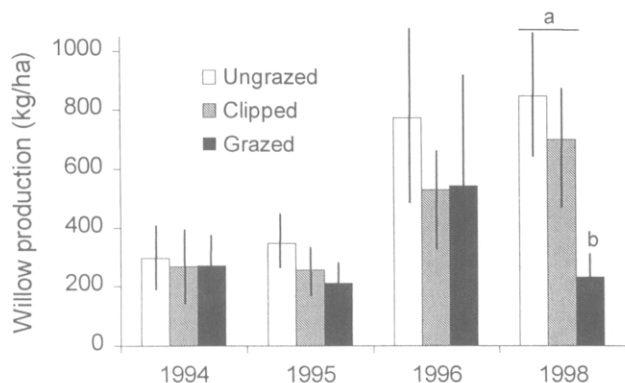


Fig. 4. Willow production (kg/ha) under different grazing treatments (different letters denote significant difference, $P < 0.02$) on elk winter range of Rocky Mountain National Park, Colorado.

evident 4 years post-treatment. There was an interaction effect between year and herbivory treatment for willow production ($P < 0.001$). After 4 years of rest from grazing, willow production had increased by 209% (Fig. 4). Willows browsed by elk were shorter than those protected or treated with clipping ($P < 0.002$) after only 2 years (Fig. 5). Willow leader lengths were shorter ($P = 0.033$) under grazed (17.5 ± 2.4 cm; $\bar{x} \pm \text{SE}$) and ungrazed (15.9 ± 2.4 cm) treatments than clipped treatments (23.1 ± 1.9 cm) in 1998. Overall leader lengths were greater ($P = 0.001$) in Moraine Park (23.2 ± 2.0 cm) than Horseshoe Park (14.9 ± 1.4 cm). In 1996, there was an

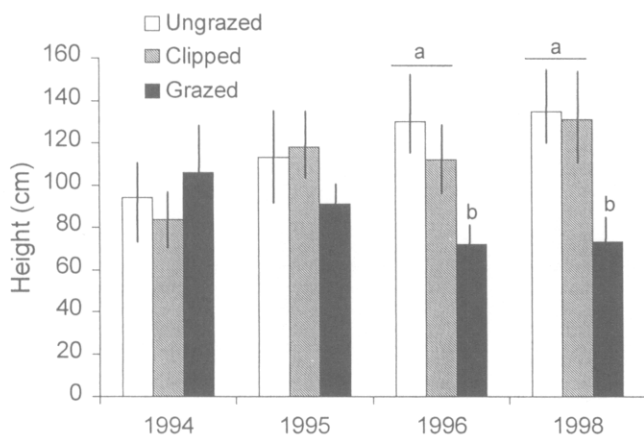


Fig. 5. Average heights of willows under different grazing treatments on elk winter range of Rocky Mountain National Park, Colorado.

interaction effect on leader length between herbivory treatment and location ($P = 0.021$) because all browsed leaders of willows under grazing were shorter in Moraine Park. All clipped willow leaders in Moraine Park were longer than clipped willow leaders in Horseshoe Park. Willow catkin production (catkins/ m^3 of shrub canopy volume) was ~70% lower under clipped (21.2 ± 3.5) and grazed (16.8 ± 6.1) than the ungrazed (69.0 ± 13.6) treatment.

Herbaceous standing crop biomass (graminoids + forbs) in both grazed and clipped treatments was 18–29% lower than in the ungrazed treatment by the fourth year post-treatment ($P = 0.016$; Fig. 6). While we did detect a pre-treatment difference in herbaceous standing crop biomass in 1994 with higher biomass in grazed sites (mainly attributed to grazed sites in Horseshoe Park), this difference was no longer significant by 1996. Percent basal cover of grasses and bare ground were greater ($P < 0.001$ and $P = 0.036$, respectively) in grazed sites. Mean cover of bare ground was $7.72 \pm 2.16\%$ in grazed as opposed to $3.10 \pm 1.62\%$ in ungrazed sites. Shrub cover ($P = 0.004$) and litter cover ($P < 0.001$) were lower under grazing. Less litter accumulated ($P < 0.009$) in grazed and clipped plots by 2 years post-treatment.

The water impoundments early in the growing season did not have any impact on willow production (Fig. 7). Willow production was greater in tall sites than either short-watered or short-control willow sites in 1994–1996 ($P < 0.001$); however, in 1998, this difference was not significant ($P = 0.118$). The height differences selected at the start of the study were maintained, despite water impoundment, and heights were greater ($P < 0.036$)

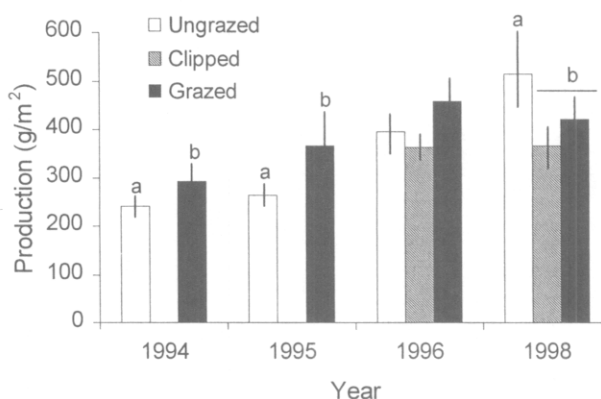


Fig. 6. Annual herbaceous production under different grazing treatments on elk winter range of Rocky Mountain National Park, Colorado (different letters denote significant difference, $P < 0.10$).

in tall sites than short-control or short-watered sites in all years.

Herbaceous standing crop biomass response to the water impoundment was difficult to interpret. At the onset of the study in 1994, herbaceous biomass was greater in short willow sites destined for water impoundments than other short willow sites. However, in 1995, the first year of damming, herbaceous biomass was, on average, 30% greater ($P = 0.006$) in tall willow sites, than both watered and control short willow sites. Following 2 and 4 years of water impoundment, in 1996 and 1998, biomass in short-watered sites was significantly greater than in short-control sites ($P = 0.051$ and $P = 0.036$), and exceeded tall sites (though not significantly so) both years (Fig. 8). This effect may have been due to *a priori* site differences between short-control and short-watered sites, or a response to water impoundment on the sites.

Shrub production and herbaceous standing crop biomass responded to total March–September precipitation, but this response fit a quadratic curve well in most cases (r^2 ranged from 0.44 to 0.94), implying that perhaps there is a threshold level of precipitation beyond which herbaceous production did not increase. However, the year of highest precipitation, 1995, also had a shortened growing season (L. Zeigenfuss, U.S. Geological Survey, personal observation) due to late warming. This may also have contributed to the lowered production during this year. In 1998, litter accumulations were also significantly greater in short-watered and tall sites than short-control sites, likely resulting from increased production in 1997.

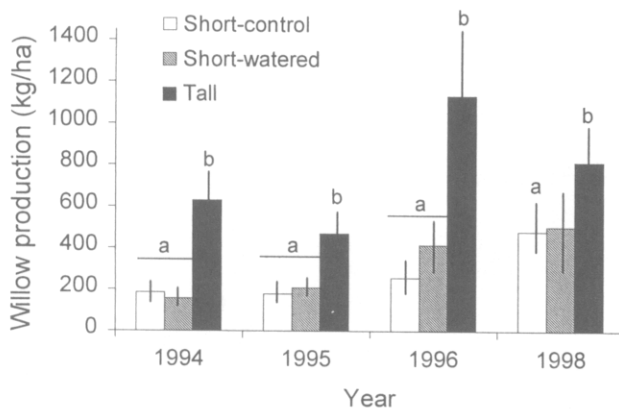


Fig. 7. Willow production (kg/ha) under different water treatments in willow communities on elk winter range of Rocky Mountain National Park, Colorado (different letters denote significant difference, $P \leq 0.05$).

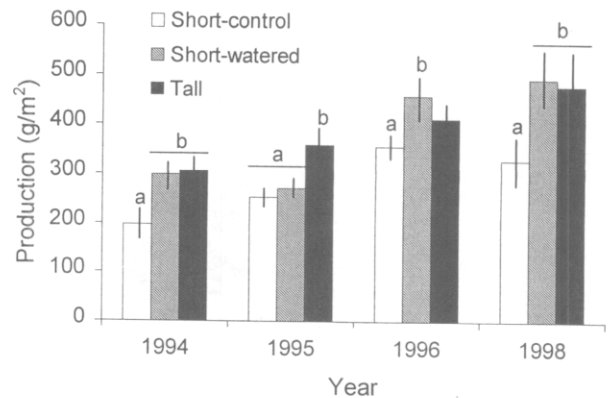


Fig. 8. Herbaceous production in willow sites with different water treatments on elk winter range of Rocky Mountain National Park, Colorado (different letters denote significant difference, $P \leq 0.05$).

Depth to water table in June and July was weakly correlated to herbaceous standing crop biomass and current annual growth of willows, but the percent of variation explained was very low (r^2 ranged from 0.04–0.06). For herbaceous plants, the association was positive, with consistently higher production with higher water tables (Fig. 9a). However, the influence of water on willow growth was difficult to interpret. While the highest production levels were achieved in sites with the highest water tables, overall, the association was slightly negative. When the data were separated by drainage, we found that most of this negative association was attributable to the Moraine Park sites, which had fewer wells, particularly in tall willow sites, and less variation in water table, with no dry sites, and few wet sites (Fig. 9b–c).

N content of graminoids and forbs was lower ($P = 0.007$ and $P = 0.080$, respectively) in clipped than grazed or ungrazed treatments (Table 3). Dry matter digestibility of graminoids was greater under grazing (Table 3). Graminoid N content increased and total non-structural carbohydrates decreased when sites were dammed as well ($P = 0.053$; Table 4).

N content of *S. monticola* and *S. planifolia* was lower under grazing and clipping, but only significantly so in *S. monticola* ($P = 0.035$) and only in winter twigs (Table 5). Summer willow twigs and leaves did not vary in N content between treatments. Grazing led to lower percent dry matter digestibility of willows, but these values were only significantly lower ($P = 0.035$) in winter twigs of *S. planifolia* (Table 5). Calcium and potassium concentrations of *S. monticola* ($P < 0.02$; Table 5) were

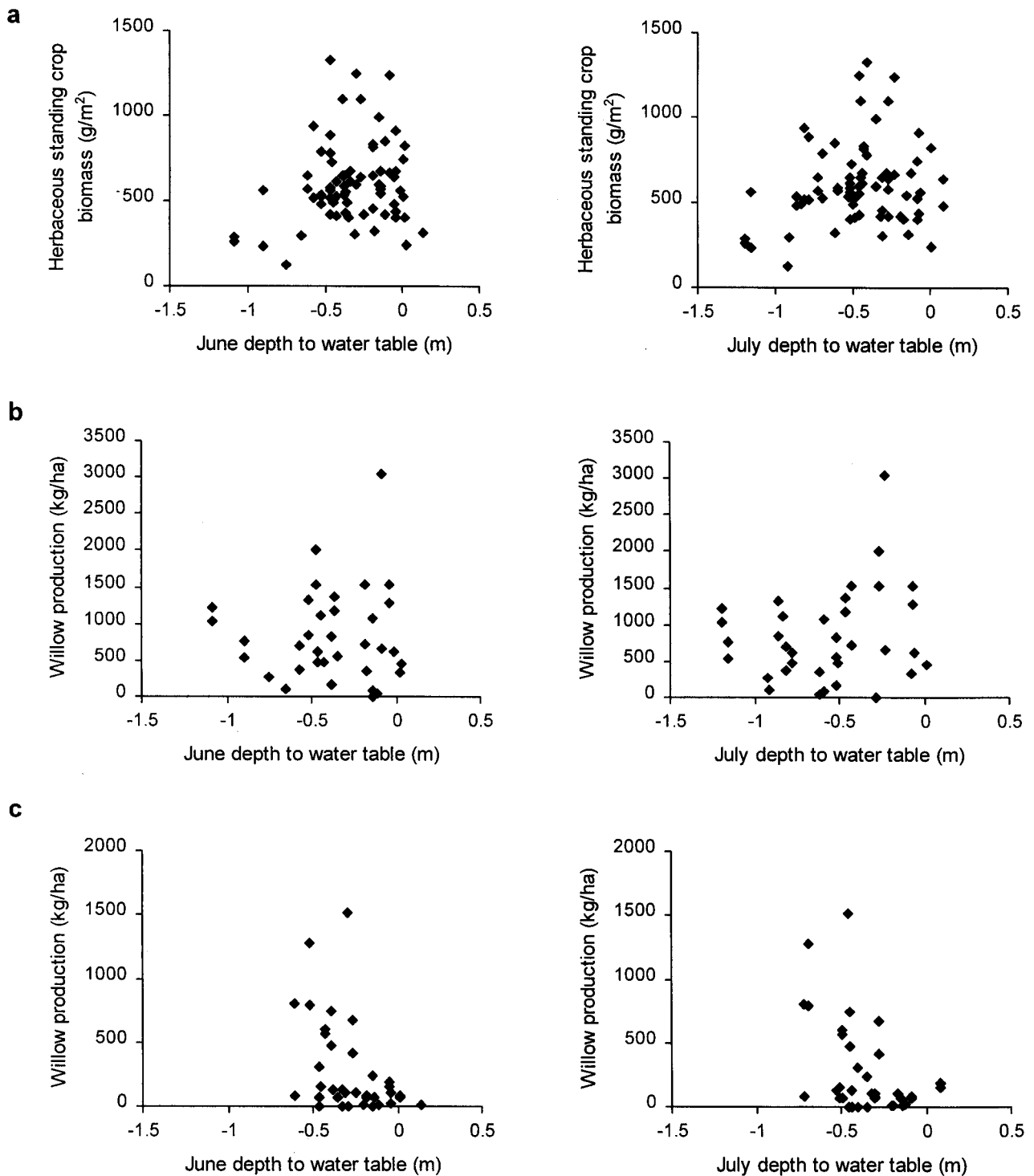


Fig. 9. Correlation of depth to water table with herbaceous biomass (a) and willow production in Horseshoe Park (b) and Moraine Park (c).

Table 3. Nutrient content of herbaceous plants under different herbivory treatments on willow sites on elk winter range of Rocky Mountain National Park, Colorado, 1998.

	Graminoids			Forbs		
	Ungrazed	Clipped	Grazed	Ungrazed	Clipped	Grazed
Carbon (%)	44.26	44.35	44.10	43.56	42.43	42.32
Nitrogen (%)	1.74	1.48 ^a	2.00	2.48	2.03 ^a	2.51
Dry matter digestibility (%)	54.72	55.29	57.16 ^a	75.00	69.96	74.81
Total non-structural carbohydrates (%)	12.12	13.83	11.78	11.78	9.55	9.00

^aDifferent from other treatments at $P \leq 0.10$.

greater under grazing. Phosphorus concentration was lower under both clipped and grazed for *S. monticola* and *S. planifolia* ($P < 0.10$; Table 5). N and C content of willows were not affected by water treatments. Concentrations of magnesium and potassium were higher in winter twigs of *S. monticola* and *S. planifolia* in tall sites ($P < 0.050$; Table 6). Phosphorus content of *S. monticola* was greater in both tall and short-watered sites ($P = 0.090$).

An interaction effect between herbivory and water treatments was noted for *S. geyeriana*. Willows of this species in tall sites that were subjected to grazing and clipping had higher potassium concentrations than did willows in short-control sites subjected to herbivory ($P = 0.030$). Iron concentrations were also higher in *S. geyeriana* plants subjected to elk grazing in short-control sites ($P = 0.048$).

Only a few significant differences in species composition were found due to herbivory in willow sites, and all were in forbs. Grazed sites had more *Solidago* spp. ($P = 0.048$), while ungrazed sites had more bluebell (*Mertensia ciliata*) ($P = 0.076$). Interestingly, one species, false Solomon's seal (*Maianthemum stellatum*), showed an increase ($P = 0.034$) under clipping.

Plant Production Responses to Burning and Herbivory in Bitterbrush Sites

Burning resulted in a reduction of total shrub canopy volume and area ($P < 0.013$; $P < 0.021$) in 1996 and 1997 (Fig. 10), as was expected from the initial consumptive effects of fire. However, resprouting from burned plants was evident in all sites. Production of *Purshia tridentata* was not different in 1996, but production was six times greater ($P = 0.006$) in unburned sites than burned sites

by 1997, suggesting that plant mortality took place during the first year following the fires. Many dead bitterbrush plants were observed on the burned sites in 1997 as well. No other significant effects of grazing on upland shrub production variables were observed.

Burning had no significant impacts on total herbaceous production, graminoid production, or forb production ($P > 0.10$) in these bitterbrush sites (Fig. 11); however, production was greater ($P = 0.077$) in ungrazed sites (pooled over burning treatment) by 1997. Herbaceous litter had increased significantly ($P = 0.003$) in ungrazed treatments by 1997. Increases in graminoid production occurred in 1995–1997 when compared to 1994, but these differences were not linked to burning or grazing treatments and were most likely due to the low precipitation that year.

Needle-and-thread grass (*Stipa comata*) had significantly less ($P = 0.063$) production in 1997 in plots that were burned and was greatest in unburned, grazed treatments. Percent cover of *Artemisia ludoviciana* and *Eriogonum umbellatum* was greater in ungrazed than grazed sites; however, no other significant differences in percent cover or abundance of species were observed.

No differences in nitrogen content, dry matter digestibility, or total non-structural carbohydrates could be found to be attributable to burning. However, percent carbon content of grasses was greater in burned treatments (45.01 ± 0.25 vs. $44.43 \pm 0.18\%$). Nitrogen content and dry matter digestibility were higher ($P = 0.090$ and $P = 0.087$ respectively) in grazed grasses ($n = 1.24 \pm 0.09\%$; DMD = $46.55 \pm 1.73\%$) than ungrazed grasses ($n = 0.98 \pm 0.11\%$; DMD = $41.77 \pm 94\%$) when pooled across burning treatments. Dry matter digestibility was also greater ($P = 0.032$) in grazed forbs ($59.68 \pm 2.49\%$) compared to ungrazed forbs ($52.34 \pm 1.73\%$).

Table 4. Nutrient content of herbaceous plants under different water treatments on willow sites on elk winter range of Rocky Mountain National Park, Colorado, 1998.

	Graminoids			Forbs		
	Short-control	Short-watered	Tall	Short-control	Short-watered	Tall
Carbon (%)	44.38	44.19	44.15	44.50 ^a	42.43	41.34
Nitrogen (%)	1.53 ^a	1.85	1.84	2.47	2.28	2.27
Dry matter digestibility (%)	56.54	54.20	54.43	70.96	73.00	75.80
Total non-structural carbohydrates	15.5 ^a	11.21	11.02	9.95	10.66	9.90

^aSignificantly different from other treatments ($P \leq 0.10$).

Discussion

Elk populations in RMNP decreased plant productivity in willow communities. Elk herbivory is the primary factor driving productivity declines, in particular, the shorter stature of many willows. Although an interaction effect between herbivory and water table depth in our experimental manipulations was not found, this may have been due to our small samples size ($n = 4$) and high sample variance, incorrect assumptions as to site-specific water table differences, relatively short time frame (4 years post-treatment) for measurement of effects, and the relatively short-lived and localized nature of our water impoundments. Our inferences as to water dynamics were limited by the smaller number of wells in Moraine Park, particularly in tall willow sites, and the fact that our sampling did not include dry years (1995–1999 were years of average or above-average annual precipitation). This problem was further confounded by the positive correlation of elk density with water table height found in these sites (Singer et al., this volume). Higher densities of elk in locations with higher water tables may mean the negative effects of elk herbivory on plant production are overwhelming any positive influence of higher water tables in these areas. Comparing grazed sites in years of different growing season precipitation further emphasized the importance of the amount of available water to plant production. Production was much lower during 1994 in our study area – a year with lower than average precipitation.

Herbivory by ungulates, such as elk, can influence many aspects of plant structure, growth, and net primary productivity. Net primary productivity can either increase or decrease as a result of ungulate herbivory (McNaughton 1979; Painter and Belsky 1993). In

RMNP, productivity increased when plants were protected from grazing. This trend was obvious starting in 1996 and the effect was significant by the fourth and final year of our study. Based on observation of exclosures in RMNP and YNP (this study; Singer et al. 1994, 1998b), we expect continued increases in canopy coverage and annual production within protected sites for some years. Herbaceous production may decline as increasing shrub canopy takes over areas or shades out understory herbs.

The effect of our clipping treatment on herbaceous biomass indicates that increased grazing pressure could further depress plant productivity in these communities. Willow production and average heights were lower in clipped than unclipped treatments, and lowest in sites grazed by elk. The timing of clipping vs. elk herbivory may explain the lesser negative response to clipping. By the end of the study, it became apparent that elk remove plant material during the spring, after the emergence of new shoots and leaves, as well as during winter dormancy, which was the period when the clipping treatments were conducted. This difference could account for the greater willow productivity, longer leaders, and greater heights observed under the clipping treatment compared to elk grazing. However, the decrease in catkin production was similar under clipping to the grazed treatment, leading us to conclude that winter clipping and browsing have equivalent effects on seed production.

Ungulate grazing and hoof action resulted in more bare ground and soil compaction on the study sites. There may possibly be higher sediment yields from the grazed sites. Any increase in bare ground could result in a warmer soil microclimate. Warmer soil, if moisture is equivalent, could result in increased N mineralization

Table 5. Nutrient content of willows under different herbivory treatments on willow sites on elk winter range of Rocky Mountain National Park, Colorado, 1998.

	<i>Salix geyeriana</i>			<i>Salix monticola</i>			<i>Salix planifolia</i>		
	Ungrazed	Clipped	Grazed	Ungrazed	Clipped	Grazed	Ungrazed	Clipped	Grazed
Winter									
Carbon (%)	52.04	51.84	51.83	51.24	51.49	50.81 ^a	50.80	50.86	50.43
Nitrogen (%)	1.14	1.15	1.08	1.18 ^a	1.10	1.08	1.25	1.19	1.10
Dry matter digestibility (%)	37.20	37.51	36.06	36.26	35.84	35.0	34.60	33.79	32.40 ^a
Calcium (mg/L)	0.61	0.64	0.65	0.71	0.68	0.81 ^a	0.62	0.68	0.65
Potassium (mg/L)	0.23	0.26	0.25	0.22	0.21	0.27 ^a	0.28	0.24	0.30
Phosphorus (mg/L)	0.13	0.14	0.13	0.13 ^a	0.12	0.12	0.14 ^a	0.13	0.13
Summer									
Carbon (%)	50.97	51.09	50.50 ^a	48.95	48.93	48.73	49.77	49.68	49.43
Nitrogen (%)	1.68	1.72	1.71	1.73	1.78	1.74	1.70	1.72	1.79
Dry matter digestibility (%)	42.22	43.12	41.11	42.59	43.08	41.02	40.43	40.39	38.17

^aDifferent from other treatments at $P < 0.10$.

Table 6. Nutrient content of willows under different water treatments on willow sites on elk winter range of Rocky Mountain National Park, Colorado, 1998.

	<i>Salix geeyeriana</i>			<i>Salix monticola</i>			<i>Salix planifolia</i>		
	Short-control	Short-watered	Tall	Short-control	Short-watered	Tall	Short-control	Short-watered	Tall
Winter									
Dry matter digestibility (%)	36.46	38.14	36.16	35.88	35.48	35.73	34.20	32.49	34.10
Potassium (mg/L)	0.19	0.23	0.32	0.19	0.22	0.28 ^a	0.25	0.24	0.34 ^a
Phosphorus (mg/L)	0.12	0.13	0.15	0.11 ^a	0.12	0.13	0.13	0.12	0.14
Magnesium (mg/L)	0.12	0.14	0.15	0.13	0.12	0.15 ^a	0.12	0.11	0.15 ^b
Summer									
Dry matter digestibility (%)	42.45	41.88	42.12	42.60	39.78 ^a	44.30	39.76	39.54	39.68

^aDifferent from other treatments ($P < 0.10$).^bDifferent only from short-watered ($P < 0.10$).

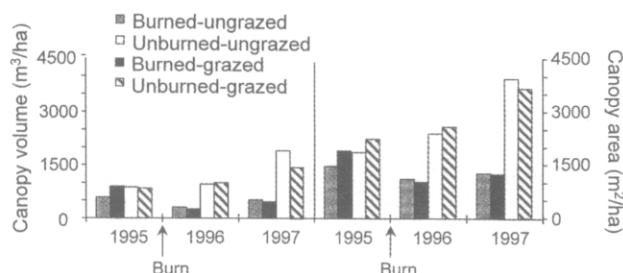


Fig. 10. Annual total shrub canopy volume (m^3/ha) and area (m^2/ha) responses to burning and grazing treatments in bitterbrush sites on elk winter range in Rocky Mountain National Park, Colorado.

on grazed sites. While we did find evidence of increased percent bare ground in grazed willow sites vs. protected areas, the mean bare ground was only 7.7%. Studies conducted in concert with ours found no increase in N mineralization on grazed sites compared to sites protected for either 4 years or 36 years (Binkley et al., this volume; Menezes et al. 2001). Percentage bare ground was significantly lower in one of two upland shrub communities protected from grazing for 36 years, but not in a wet meadow community (Schoenecker et al., this volume). Percentage spring soil moisture ranged from 1–10% greater in areas protected from grazing for 36 years (D. Binkley, Colorado State University, unpublished data), but no differences in soil moisture were found between 4-year-old exclosures and grazed areas (R. Menezes, Natural Resources Ecology Laboratory, unpublished data). Summer soil temperatures were 1–5 degrees cooler in the 36-year-old exclosures (D. Binkley, Natural Resources Ecology Laboratory, unpublished data).

Ungulates can influence the natural heterogeneity of N in the landscape by changing litter quality, thereby affecting N mineralization rates, and by adding readily available N to the upper soil levels in the form of urine and feces (Hobbs 1996). Elk grazing increased N and other nutrient content and digestibility of forages in other study areas (Frank and McNaughton 1992; Singer and Harter 1996). Increases in graminoid N concentration under grazing in willow and bitterbrush sites indicate that elk are having a positive influence, at least in the short-term, on N cycling in RMNP willow communities.

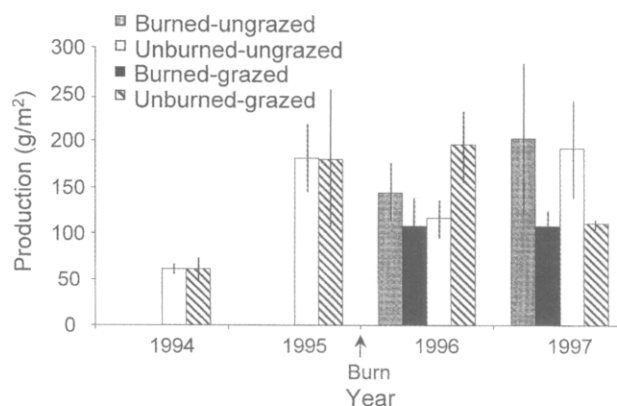


Fig. 11. Herbaceous production (g/m^2) in response to grazing and burning treatments in bitterbrush sites on elk winter range in Rocky Mountain National Park, Colorado.

N levels decreased in the clipped treatment, which seems counter-intuitive until the lack of additions of either urine and feces, or decomposing plant litter, is considered. The increased percent dry matter digestibility and concentration of important forage nutrients (such as calcium) under grazing may create heavily grazed patches, which attract continued use. Such “grazing lawns” have been argued to cause evolution of plants to withstand long-term heavy grazing (McNaughton 1986). In the short-term (i.e., less than an evolutionary time scale), the effects of heavy grazing may be reduced productivity or species shifts. However, some effects of elk on vegetation and soil and nutrient processes should be considered normal and natural in a national park ecosystem in which elk are a native species.

Hydrologic changes may be exacerbating the effects of elk herbivory in RMNP, despite our ability to determine significant response of plant production to water table dynamics. Hydrologic changes over the last 50 years include a 69% decrease in surface area of water in Moraine Park and a 47% decrease in Horseshoe Park (Peinetti et al., this volume). This decline has been attributed primarily to decreases in beaver activity and beaver dams. Concurrent declines in willow cover of 20% were observed during the same period. Decline in cover of tall willows ranged from 54–65% (Peinetti et al., this volume). Elk populations increased during the same period from ~700 to 3,000 (Lubow et al. 2002). Beaver activity on the surveyed streams has declined substantially over the past 17 years, contributing to a substantial decline since 1940. Actual beaver population

sizes are unknown and comparisons of population estimates derived from different surveys are problematic; however, the estimates are likely a reasonable indication of the relative population trend over time. Low winter stream flow levels, plague, tularemia epidemic, poaching, predation, and competition with deer and elk over woody browse, were suggested as factors that may have contributed to beaver declines prior to 1980. There is evidence for each of these possible causes. In 1982, the Lawn Lake dam collapsed, causing a large flood on the Fall River downstream of the Roaring River, which contributed to the large beaver decline, recorded in that drainage since 1981 (4 of 10 lodges recorded in 1981 were in the path of the flood). Since 1994, three cases of tularemia were confirmed from beaver carcasses found along the Big Thompson and Fall Rivers. Overall declines have occurred in areas lightly-used (Glacier Creek) or moderately used (Hallowell Park, Cow Creek) by elk during winter, as well as elk winter concentration areas (Moraine Park, Horseshoe Park, and Beaver Meadows).

The decline in beaver populations may also be contributing to declining willow populations under heavy elk herbivory through reduced recruitment sites. Beaver cuttings from willow often root and become established along beaver ponds, dams, and flooded channels. Old beaver ponds often provide ideal substrate for establishment of willow seedlings. The loss of beavers and their consequent effects of raising the water table and stimulation of suckering in willow following beaver cutting (Kindschy 1989) are potentially leading to lowered regeneration in willow communities.

Other limiting factors may be hydrologic changes due to human water use or a change to a warmer, drier climate over the period of decline (Singer et al. 1998b). All of the meadows in the major elk feeding areas experienced water diversions for agriculture, resort and housing developments, and irrigation along the Colorado Front Range in the past. In recent decades, 95% of the diversions in Beaver Meadows, and 80% of those in Horseshoe Park have been eliminated. Only 50% of water diversions from Moraine Park have been restored (K. Czarnowski, National Park Service, personal communication). However, there is no way of knowing whether restoration of diverted water reverses changes to the ecosystem which may have occurred during years of lower water availability. The combination of climate change over the last century to drier conditions, in concert with heavy elk herbivory, may also contribute to willow decline. Analysis of climate records around Estes

Park shows a temperature increase of 0.89°C and precipitation decreases of more than 1 cm over the last century (Singer et al. 1998b).

Whatever the cause of the decline, the decreasing numbers of beaver have altered hydrology on the elk winter range in the park. Areas formerly occupied by beaver are now merely dry channels that fill with water only during spring runoff or occasional heavy rain events. The reduction in length of streams on the winter range (44–56% less) due to channel straightening and simplification are attributed to the beaver decline (Peinetti et al., this volume). Several decades following beaver abandonment, water and/or nutrient-stressed willows may become less able to recover from tissue losses due to ungulate herbivory (Kozłowski 1971; Gurchinoff and Robinson 1972; Bryant and Kuropat 1980).

We did not detect any shifts in species composition to more palatable, grazing-resistant species due to elk herbivory. While it might be argued that our time frame was too short to detect shifts in species composition, other studies of long-term grazing near three exclosures of 36 years in the same areas of RMNP have found few species effects (Stohlgren et al. 1999). One species that increased under protection in our study, *Mertensia ciliata*, was also one of only 24 species found exclusively within 36-year old exclosures by Stohlgren and others (L. Schell, Natural Resources Ecology Laboratory, personal communication). A few significant differences in species composition that were found in willow sites were associated with location (Moraine Park vs. Horseshoe Park) or water treatment (short-control vs. short-watered or tall). Because many of these differences have more to do with plant population distributions, former agricultural practices, or suitable habitat (some plants naturally grow better in a wetter or drier habitat), we will not discuss them here, except to mention that increases in water tables due to reintroduction of beaver to some of these areas would likely have some consequent effects on species composition.

Management Recommendations

Reducing elk numbers and/or reducing elk concentrations, altering the timing of use of willows, or exclusion of elk from willow communities will likely result in increases in plant productivity. Fencing parts of these communities to encourage greater seed production and establishment, and to allow some individual willows to increase in size beyond the reach

of elk, may help sustain willow communities over the long term. Our study showed increased height of willows within 2 years of protection from browsing and increased catkin production within 4 years.

Reintroduction or restoration of beaver populations to parts of this range, or artificial manipulations of hydrology in willow areas to simulate beaver ponds will allow these sites to sustain high levels of herbivory, and will hasten height recovery of any willows that are protected from herbivory for 5–10 years. While our study was inconclusive as to the contribution of the water table to production, hydromanipulations could be aimed at catching and holding runoff to provide more water earlier in the growing season. Simulated beaver cuttings (Kindschy 1989) to stimulate suckering, and plantings from cuttings, could be used within protected areas to increase willow establishment.

Protection from browsing and water enhancement for short periods (less than 10 years) alone would not necessarily lead to sustainable willow communities. Management to encourage elk movement away from willow communities would also be necessary. Elk tend to be concentrated in certain areas of the range, such as Moraine Park. Shrub consumption levels reflect these increased elk densities (Singer et al., this volume). Management of elk to decrease these concentrations could lead to lowered levels of consumption, and thus increased plant productivity and potentially a return to larger communities of tall, healthy willows.

Prescribed fire had little effect on forage production or quality in upland bitterbrush communities. This may have been because the majority of the fires were conducted in spring when there was little fuel left to carry a fire. However, a large natural fire in Yellowstone had few effects on upland grasslands, with biomass increases only evident 2 years post-fire, and little change in nutrient concentration or digestibility of forages (Singer and Harter 1996). As the park's prescribed fire program expands, further study of the interaction of elk herbivory and fire effects are recommended.

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